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The Cognitive Animal

Empirical and Theoretical Perspectives on Animal Cognition

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19 Cognition as an Independent Variable: Virtual Ecology

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On close examination, human cultural artifacts bear the unmistakable impress of the structure of the human mind; our tools, habitations, and methods of communication have been molded to suit the strengths and limitations of the human cognitive system (Norman 1988). It has not commonly been emphasized, however, that similar shaping processes have taken place over the course of biological evolution in response to the cognitive features of other, nonhuman species (Bonner 1980; von Frisch 1974).

Cognitive influences are particularly evident in the modifications of color patterns and behavior of prey species that take advantage of biases and constraints in the perceptual systems of their principal predators. For example, avoidance learning by predators contributes to the evolution of aposematic, or warning, coloration in many distasteful or poisonous species (Guilford 1990; Schuler and Roper 1992); Batesian mimicry (Bates 1862), in which palatable prey evolve to imitate the appearance of aposematic species, takes advantage of the predator's tendency to generalize stimuli (Oaten et al. 1975). But perhaps the most striking illustration of the effects of predator cognition on prey appearance is the large number of species of cryptically colored insects that are polymorphic, with a single species occurring naturally in a variety of disparate forms.

Cryptic prey polymorphism is common among grasshoppers, leafhoppers, and walking-sticks, but it is particularly characteristic of lepidoptera (Poulton 1890). Many moths have evolved cryptic coloration to avoid bird predation while they rest on tree trunks during the daytime, and polymorphism is pervasive among these species. In North America, roughly 45 percent of the noctuid moths in the genus *Catocala* are polymorphic, with some species occurring in as many as nine different morphs (Barnes and McDonough 1918). In other branches of the same

family, the degree of morphological variation can be even more extreme. Adults of the army cutworm, *Euxoa auxiliaris*, are almost continuously variable in appearance.

In 1890, Poulton remarked on the high frequency of polymorphism among cryptic insects and formulated a remarkably perceptive explanation for the phenomenon. He said that in polymorphic species, "the foes have a wider range of objects for which they may mistake the moths, and the search must occupy more time, for equivalent results, than in the case of other species which are not polymorphic" (Poulton 1890, p. 47). His implications are, first, that polymorphism is an adaptive response to the foraging behavior of the predator and by extension, of the cognitive processes that determine successful visual search. Second, the selective advantage of polymorphism results from the fact that it is harder and more time-consuming to search for several things simultaneously than to search for only one.

The cognitive process involved appears to be a transitory increase in a predator's ability to detect cryptic prey when items of a similar appearance are encountered in rapid succession (Pietrewicz and Kamil 1979; Bond and Riley 1991; Reid and Shettleworth 1992), a phenomenon that has been termed "hunting by searching image" (Tinbergen 1960). As a result of the shift in detectability, visual predators tend to search for only a limited number of prey types at any moment in time, focusing on the most common prey available and effectively overlooking the others (Tinbergen 1960; Bond 1983; Bond and Kamil 1999).

The ecological consequence of this perceptual bias is known as apostatic selection (Clarke 1962, 1969), and it has been suggested to be the primary mechanism for maintaining stable prey polymorphism. If predators tend to search most effectively for prey types they have recently

found, then the more common any given prey type is, the more heavily it will be preyed upon. Thus as a prey type becomes more common, predation on it increases while the predation pressure on rarer types declines. Common morphs experience relatively higher predation rates and decline in numbers, while rarer ones become more common. The outcome should be a stable configuration of prey types with a much higher degree of morphological diversity than would have been the case in the absence of predatory cognitive biases.

Apostatic selection is an elegant theory, but until recently, empirical support has been only fragmentary and indirect, primarily because experimental evolutionary ecology is an exceedingly difficult undertaking. When predators and prey are brought into the laboratory, the simplified environment interferes with normal population cycles (Murdoch 1969; Murdoch and Oaten 1975). And when evolutionary effects are sought in the field, limited experimental control reduces one's ability to make causal inferences. Although there are many documented instances of apparently stable polymorphisms and a fair amount of field experimentation indicating that predators tend to feed preferentially on more common morphs (Clarke 1969; Allen 1988; Cooper 1984; Cooper and Allen 1994), it has proven impossible to isolate the role of predation in the production and maintenance of prey polymorphism. What has been needed is a method for studying the detection of cryptic prey that allows the isolation of the many variables that can affect the decisions of a predator, including recent experience, and then allows predation to feed back onto the prey population. We have developed such a technique, which we call "virtual ecology," a novel paradigm that combines populations of artificial prey organisms with the foraging behavior of real predators.

Our methods derive from an established experimental system. In North America, noctuid moths are commonly preyed on during the day-time by blue jays (*Cyanocitta cristata*), which are

the only avian predator that seems able to break the crypsis and find these insects while they are at rest on tree trunks. In a series of experiments in the 1970s, Pietrewicz and Kamil (1977, 1979) were able to show that jays in operant chambers exhibited the same impressive detection abilities when they were required to locate cryptic moths in slide images, and that the parameters of their search for moth images in the laboratory provided a satisfactory emulation of natural foraging behavior. In particular, (1) when the crypticity was increased, the birds were both slower and less accurate at detecting the moths; (2) responses to the moth images were substantially faster than those to the displays without moths, indicating an exhaustive, self-terminating search; and (3) the birds showed better detection after a run of a single type of moth than during random presentations of differing moth types, which has come to be considered a criterion for the use of searching images (Blough 1991; Bond and Riley 1991; Reid and Shettleworth 1992; Langley 1996; Kono et al. 1998; Bond and Kamil 1999).

For our purposes, photographs of moths on tree trunks were not sufficient. To explore evolutionary issues, we needed standardized backgrounds and much greater control of the features of the prey stimuli. So we undertook to convert this natural predator-prey system into something that was more amenable to digital manipulation, while retaining the essential features of the interaction. Our compromise was to take photographs of *Catocala* moths, render them in gray scale, and reduce them to a 16×16 pixel image, producing virtual moths (for a similar approach, see Plaisted and Mackintosh 1995). For the backgrounds, we reverse engineered the evolutionary process, generating fractal backgrounds based on the distribution of gray levels in the moths, which allowed us to titrate the difficulty of the detection task by manipulating the generating distributions (figure 19.1).

As in the earlier experiments using photographs, the moths were presented one at a time to blue jays in an operant chamber. In each trial

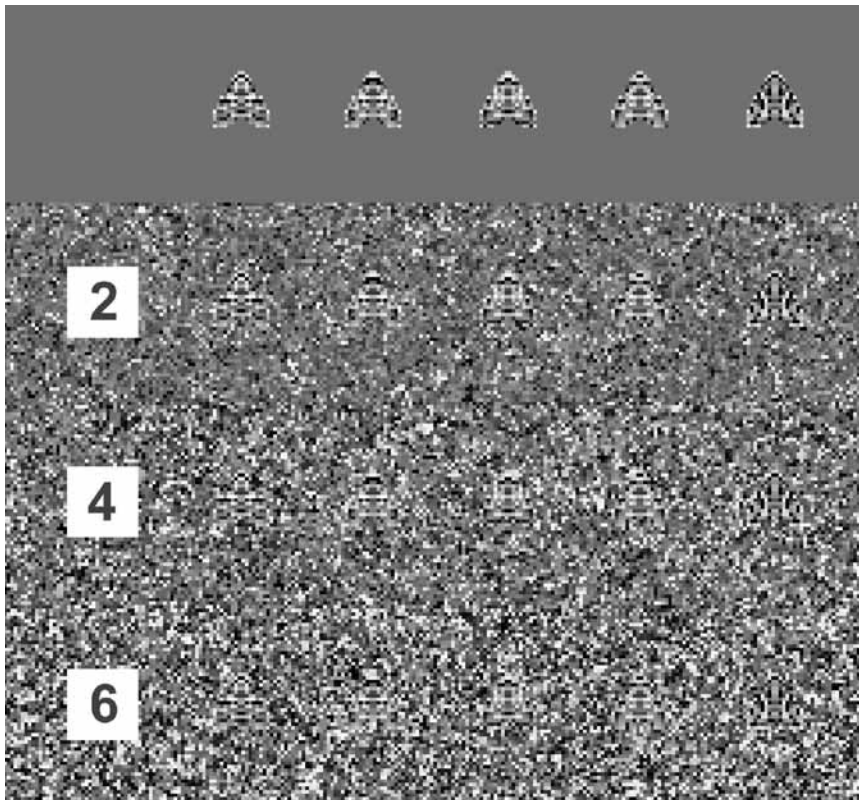


Figure 19.1

The five types of digital moths used in the virtual ecology experiments (moths 1 to 5, from left to right), presented against backgrounds of three levels of crypticity to illustrate the difficulty of the detection task. When projected on a computer monitor, the moths were about 6 mm high.

there either was or was not one moth image embedded in one of two fields of cryptic background on a computer monitor. If the bird correctly detected a moth, it pecked it and was rewarded with a food pellet. If the bird did not find a moth, it pecked a central green circle, in which case the next trial began immediately. The bird was never informed if it overlooked a moth, and if it pecked an area of background with no moth present, the time to the next trial was substantially delayed. Searching image experiments

using this methodology showed results that were equivalent to those produced using photographs (Bond and Kamil 1999), which encouraged us to generate additional novel forms with similar attributes and to develop populations of digital moths that would interact with the real jays in a dynamic virtual ecology.

Our first virtual ecosystem was a moth population of 240 individuals distributed among three fixed, disparate morphs. The population was exposed to predation by six blue jays. Over the

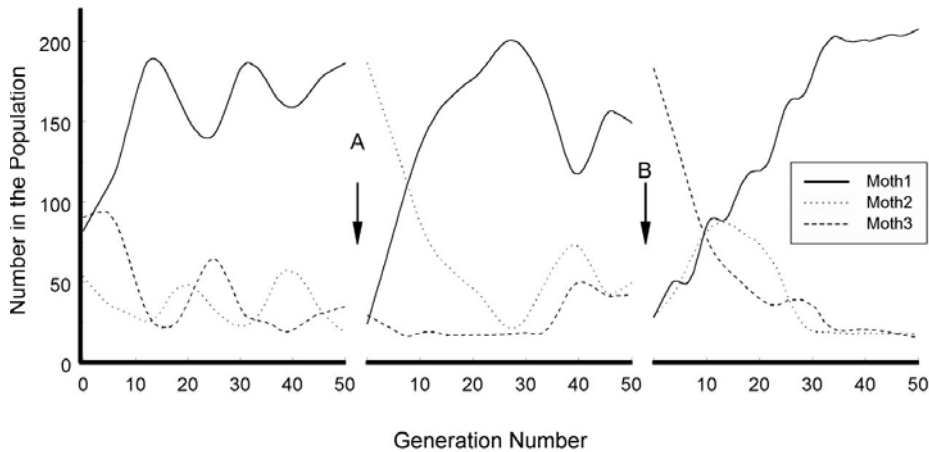


Figure 19.2

Population numbers of three morphs in three successive replications of the virtual ecology procedure. At point A, the second replication began; at point B, the third replication began. Curves were smoothed with weighted least squares using an 8-generation window

course of each daily session, each moth was presented once to one of the predators. Those moths that were detected were considered killed and were removed from the population; those that were overlooked survived and were proportionately cloned to create a new set of 240 individuals for the following day. Each day thus constituted a generation, and the makeup of the population at any given time was a direct reflection of the previous history of predation. We conducted three replications of this selection process, each running for 50 generations, but beginning with different starting conditions. In each case the relative numbers of the three moth types rapidly converged on approximately the same equilibrium values (figure 19.2). Analysis across replications of the rates of detection of each morph demonstrated that this equilibrium was the result of the predicted negative feedback between prey numbers and the probability of detection by the jays. When a moth type became more common, it became more likely to be detected and this in turn made its numbers de-

crease. Our results thus clearly implicated apostatic selection and demonstrated directly that such selection by visual predators can stabilize a preexisting polymorphism (Bond and Kamil 1998).

We then went on to test the effects of jay predation on the establishment of a novel prey type. If a new morph occurs in a population through immigration or mutation, its initial abundance will be low. Since local predators will have no experience with the new type, density-dependent selection should favor an increase in a new morph. We tested this by introducing a novel, fourth morph. Initially, the jays failed to detect it and it increased in abundance, briefly becoming the most common type in the population. Eventually, however, the jays learned to detect the new morph, and its numbers declined to a new equilibrium level (figure 19.3). This was not, however, the only possible outcome. When we repeated the novel prey introduction with a fifth morph that was extremely cryptic, only two of the six jays learned to detect it, and the novel

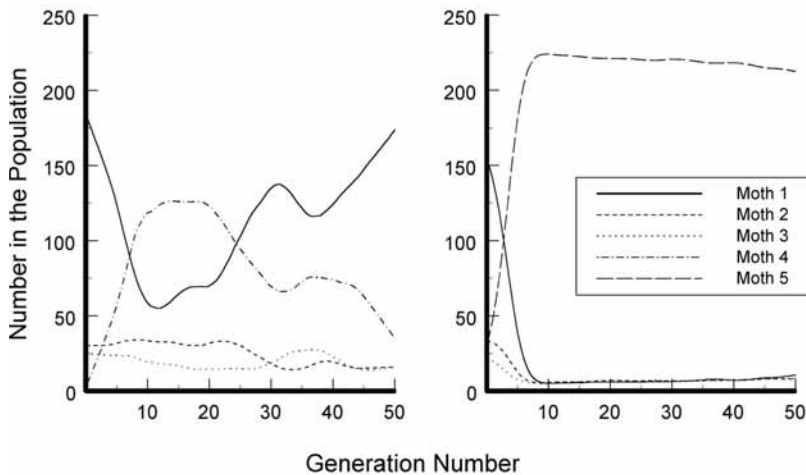


Figure 19.3

Population numbers of four morphs in the last two replications of the virtual ecology procedure. Curves were smoothed with weighted least squares using an 8-generation window. Replication 4, shown in the left panel, included moths 1 through 3 and moth 4; replication 5, shown in the right panel, included moths 1 through 3 and moth 5.

morph quickly came to dominate the population, essentially driving the other types to extinction (figure 19.3) (Bond and Kamil 1998). This result demonstrated that the selective effects of predation can be as powerful in virtual ecology as in the real world.

These results encouraged us to undertake an exploration of the role of predation in the origin of prey polymorphism, testing whether the process of predatory search, in and of itself, will tend to select for color polymorphism in an initially monomorphic population. This is a much more complex issue, since it requires a virtual genetics. We have developed an algorithm loosely based on current understanding of the control wing pattern development in lepidoptera, including (1) loci that code for individual patches of pattern elements, (2) loci that produce global changes in wing brightness or contrast without modifying pattern elements, and (3) linkage mechanisms that protect favorable genetic com-

binations from being lost during recombination (Robinson 1971; Nijhout 1991, 1996; Brakefield et al. 1996).

We are currently conducting experiments in which jays hunt a population in which individual moths are defined by their genotypes, and moths that survive exposure to the predators have a significantly higher probability of being allowed to breed and contribute to the next day's generation. To track the evolution of prey crypticity, we developed a crypticity index based on the correspondence between the phenotype and the background in the distribution of color and size of pixel patches (Endler 1984). The first of these studies has been completed recently (Bond and Kamil 2002) and directional selection did occur. The virtual moth populations evolved to become more cryptic and more phenotypically diverse than under appropriate control conditions. This outcome clearly establishes that our virtual ecology is at least a sufficient emulation of a real

predator–prey system. But the real power of this technique lies in its amenability to testing through simulation. Because the selective process operates on virtual prey items under software control, the role of the predator can be subsumed, for purposes of hypothesis testing, by simulations that possess varying degrees of cognitive competence. In this fashion, we have been able to focus on the specific aspects of the jay's behavior that influence the distribution of prey phenotypes.

Conclusions

The significance of a study of animal cognition is usually viewed in terms of understanding the underlying neurophysiological and behavioral mechanisms or of interpreting the adaptive significance and evolutionary history of an organism's cognitive capabilities. However, as our experiments demonstrate, an animal's cognitive characteristics themselves can have direct evolutionary consequences. These are not limited to the detection of cryptic prey. For example, in sexual selection, the preferences expressed in mate choice are clearly a function of the cognitive characteristics of the animals doing the selecting (Endler and Basolo 1998). Thus we believe that students of animal cognition can make an essential contribution to understanding the natural world by participating in the study of cognition as an independent variable in evolutionary processes.

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